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The topology and drivers of ant–symbiont networks across Europe

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ABSTRACT

Intimate associations between different species drive community composition across ecosystems. Understanding the ecological and evolutionary drivers of these symbiotic associations is challenging because their structure eventually determines stability and resilience of the entire species network. Here, we compiled a detailed database on naturally occurring ant–symbiont networks in Europe to identify factors that affect symbiont network topology. These networks host an unrivalled diversity of macrosymbiotic associations, spanning the entire mutualism–antagonism continuum, including: (1) myrmecophiles –

commensalistic and parasitic arthropods; (2) trophobionts – mutualistic aphids, scale insects, planthoppers and caterpillars; (3) social parasites – parasitic ant species; (4) parasitic helminths; and (5) parasitic fungi. We dissected network topology to investigate what determines host specificity, symbiont species richness, and the capacity of different symbiont types to switch hosts.

We found 722 macrosymbionts (multicellular symbionts) associated with European ants. Symbiont type explained host specificity and the average relatedness of the host species. Social parasites were associated with few hosts that were phylogenetically highly related, whereas the other symbiont types interacted with a larger number of hosts across a wider taxonomic distribution. The hosts of trophobionts were the least phylogenetically related across all symbiont types. Colony size, host range and habitat type predicted total symbiont richness: ant hosts with larger colony size, a larger distribution range or with a wider habitat range contained more symbiont species. However, we found that different sets of host factors affected diversity in the different types of symbionts. Ecological factors, such as colony size, host range and niche width predominantly determined myrmecophile species richness, whereas host phylogeny was the most important predictor of mutualistic trophobiont, social parasite and parasitic helminth species richness. Lastly, we found that hosts with a common biogeographic history support a more similar community of symbionts. Phylogenetically related hosts also shared more trophobionts, social parasites and helminths, but not myrmecophiles.

Taken together, these results suggest that ecological and evolutionary processes structure host specificity and symbiont richness in large-scale ant–symbiont networks, but these drivers may shift in importance depending on the type of symbiosis. Our findings highlight the potential of well-characterized bipartite networks composed of different types of symbioses to identify candidate processes driving community composition.

Key words: ant guests, commensalism, ecological network, Formicidae, host–parasite network, host switching, inquiline, microcosm, mutualism, parasite species richness.

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I. INTRODUCTION

Close associations between different species, known as symbioses, are crucial components of communities in all ecosystems. These intricate associations display a high diversity, ranging from mutually beneficial partnerships to parasitic interactions in which one species exploits another (Paracer & Ahmadjian, 2000). Interactions among species are central to ecological and evolutionary dynamics in assemblages of species that belong to different guilds and trophic levels. They are thus essential elements of the 'entangled bank' – Darwin's metaphor for the complexity and connectedness of natural systems (Darwin, 1859) – and can give rise to important stabilising feedbacks that eventually maintain diversity and ecosystem functioning (Thrall *et al.*, 2007; Bastolla *et al.*, 2009). To date, insights are derived from theory and empiricism focusing on either competition and predator–prey interactions (e.g. Hairston, Smith & Slobodkin, 1960; Pimm, 1979; Tilman, 1982) or more recently mutualistic interactions (Bascompte, Jordano & Olesen, 2006; Bascompte & Jordano, 2007; Barabás, D'Andrea & Stump, 2018; Johnson & Bronstein, 2019; Spaak & De Laender, 2020). Communities contain a wide variety of interactions, rendering the ecological network extremely complex (Newman, 2003). One important feature of complex systems is the presence of properties that emerge from interactions among the specific components of the system (Solé & Bascompte, 2006). Typically, these emergent properties result from the interaction between different network components across time and space and are difficult to predict from the specific (isolated) pairwise interactions (Vázquez, Chacoff & Cagnolo, 2009; Grilli *et al.*, 2017). Generally speaking, modular networks that are characterized by a high connectance tend to be more robust to species loss, and are less affected by disturbance (Solé & Bascompte, 2006; Olesen *et al.*, 2007). While theoretical progress has been made (Solé &

100 Montoya, 2001), the field is suffering from a lack of comprehensive and manageable
101 empirical systems. This limits empirical tests of theory (Valdovinos, 2019) and thus hampers
102 the development of effective management tools to safeguard the biodiversity and ecosystem
103 functions of natural ecosystems (De Laender *et al.*, 2016).
104 The study and interpretation of the drivers and consequences of the topology in host–
105 symbiont networks sheds light on the evolution of the strategies and traits of hosts and
106 symbionts. Moreover, this network approach may unravel general rules in community
107 assembly processes which can be compared across different types of symbionts and different
108 systems. While network studies at local scales will be informative on the local community
109 assembly processes, those reconstructed at regional or global scales will allow inference of
110 macro-ecological and evolutionary processes (Trøjelsgaard & Olesen, 2013).
111 In contrast to trophic networks, bipartite host–symbiont networks contain different kinds of
112 links, with interactions between hosts and symbionts ranging from antagonistic to mutualistic
113 (Ings *et al.*, 2009). Examples of such networks include plant–mycorrhiza and host–
114 microbiome associations. The complexity of these networks is enormous, and their
115 description is merely based on one interaction type, either antagonistic or mutualistic,
116 although theory predicts that the diversity of interaction types may be essential for community
117 stability (Fontaine *et al.*, 2011; Mougi & Kondoh, 2012; Allesina & Tang, 2015). The
118 topology of bipartite host–symbiont networks can be dissected by adopting two different
119 perspectives, i.e. that of each of the individual sets of species (hosts and symbionts). Asking
120 what factors cause a given topology is equivalent to asking, for each of the sets, what explains
121 the number of links per species and the specificity of these links, i.e. how the links are
122 distributed among species from the focal set. An example of this approach is found in studies
123 on predator–prey networks, where average web vulnerability (i.e. the average number of

predators per prey) and generality (i.e. the average number of prey eaten per predator) link the specificity of the two interacting species sets (Schoener, 1989).

A determining feature of the ecology of symbionts is host specificity, which can be quantified in host–symbiont networks by the number of links departing from a symbiont node. Yet, a measure of host specificity should ideally consider the relatedness of the targeted host species as well (Poulin & Mouillot, 2003). Generalist symbionts target multiple, unrelated host species and may gain low to high benefits in any host. Specialist symbionts, in turn, engage with one or only a few related species, and achieve high benefits with their hosts by resorting to advanced morphological, physiological and behavioural adaptations (Bronstein, Alarcón & Geber, 2006; Thrall *et al.*, 2007). Their strong specialization, however, is offset by lower population densities and higher extinction risks due to the lower availability of hosts. Several studies in host–symbiont systems clearly found that host specificity is tightly linked with fundamental ecological processes and evolutionary history. Typically, host specificity is different among cohabiting symbionts, as for example demonstrated in parasites of primates (Pedersen *et al.*, 2005) and in parasitic mites on mussels (Edwards & Malcolm, 2006). A study on moths and plants indicated that host specificity can be dependent on the type of symbiotic interaction, with pollinating moths being more specific than their parasitic leaf-feeding relatives (Kawakita *et al.*, 2010).

From the perspective of the host, it is fundamental to understand the ecological, evolutionary and environmental drivers that promote the number of associated symbionts, i.e. the number of links departing from a host node to symbiont nodes. Studies on different host–symbiont systems reported multiple host variables which correlate with parasite species richness. Generally, the makeup of symbiont communities is orchestrated by both ecological and evolutionary host factors. Body size has been identified as a key ecological factor that favours species richness (Lindenfors *et al.*, 2007) and species interactions (Werner & Gilliam, 1984).

149 Host species may be conceptualized as island habitats for symbionts and, in line with island
150 theory (MacArthur & Wilson, 1967), larger host species tend to support more symbionts
151 (Kuris, Blaustein & Alió, 1980). Symbiont richness is also expected to increase with other
152 ecological factors such as the number and variety of microhabitats offered by the host, host
153 longevity, host range, and interaction probability with other host species (Kamiya *et al.*, 2014;
154 Stephens *et al.*, 2016). Evolutionary processes may affect symbiont species richness in
155 different ways. Related hosts often show traits that are correlated throughout evolution
156 (phylogenetic correlation) which lead to similar values in species richness. However, related
157 host species may have diverged with time, whether or not in a common spatial evolutionary
158 ancestry (biogeography), but may still attract a similar fauna of symbionts as unrelated host
159 species with a similar ecology (Poulin, 1995).
160 Another pattern that emerges in host–symbiont networks is the sharing/transmission of
161 symbiont species across host species. The degree of symbiont sharing is vital as symbiont
162 transmission can connect eco-evolutionary dynamics across hosts as a result of rapid
163 symbiont spread in host populations [e.g. Jaenike *et al.*, 2010; Himler *et al.* (2011) in
164 endosymbionts]. While little is known about the proximate mechanisms by which single
165 symbionts switch between hosts, we can anticipate that host species with similar ecological
166 niches and/or a shared evolutionary history tend to have similar symbiont communities. The
167 pervasive effect of phylogenetic relatedness on symbiont sharing has for example been
168 demonstrated in bat parasites (Luis *et al.*, 2015) and in plant–mycorrhiza (Veresoglou &
169 Rillig, 2014).
170 Ant–symbiont networks are ideally suited to study which factors drive bipartite network
171 topology (Ivens *et al.*, 2016). The diversity of symbiotic associations found in ants (Kistner,
172 1982; Hölldobler & Wilson, 1990; Rettenmeyer *et al.*, 2010; Parmentier, 2020) is thought to
173 be promoted by their omnipresence in terrestrial ecosystems, their stable and climate-

controlled nest fortresses and the high number of available resources in the nest (Kronauer & Pierce, 2011). Ants interact with different types of symbionts spanning the entire parasitism–mutualism gradient. They include parasitic ants, different groups of arthropods living in the nests, mutualistic aphids and caterpillars, endoparasitic helminths, plants, bacteria and fungi (Hölldobler & Wilson, 1990). Therefore, they are promising systems to study different interaction types within a single biological system (Fontaine *et al*., 2011).

Ant–symbiont networks that have been studied recently typically deal with local interaction networks and mostly focus on one kind of symbiotic interaction in isolation, such as mutualistic plant–ant networks (Guimarães *et al.*, 2006; Blüthgen *et al.*, 2007; Dáttilo, Guimarães & Izzo, 2013; Cagnolo & Tavella, 2015), mutualistic aphid–ant networks (Ivens *et al.*, 2018) or parasite–ant networks (Elizalde *et al.*, 2018). Some studies have already covered different types of symbiotic interactions in a local network (Pérez-Lachaud & Lachaud, 2014; Rocha, Lachaud & Pérez-Lachaud, 2020) and a recent study tested different types of ant–symbiont interactions on a large scale (Glasier, Poore, & Eldridge, 2018). However, the latter study only included a limited set of interaction types and pooled interactions of well-studied bioregions with those of very poorly studied regions.

Here, we ask what factors explain the topology of ant–symbiont networks across Europe. We firstly provide a quantitative and systematic meta-analysis of the diversity of European ant–symbiont interactions. By adopting the symbiont perspective, we test the hypothesis that the type of symbiosis explains the number and identity of their host species (host specificity). More specifically, we expect that parasitic ants are more specific than the other types of symbionts. Secondly, we follow a trait-based host perspective to identify the major drivers that promote the diversity of ant–symbiont interactions and facilitate symbiont sharing. We test the hypothesis that the number of symbionts with which an ant species interacts and the number of symbionts it shares with other ant hosts depend on ecological factors (colony size,

nest type, distribution, habitat, degree of sympatry, worker size) and evolutionary drivers (phylogeny, biogeography) associated with the host species.

II. MATERIALS AND METHODS

(1) Ant symbionts

Symbionts are species that engage in a close association with a host species on which they may have beneficial, neutral or adverse effects. We limited our analyses to Europe (excluding the Canary Islands and Madeira), as knowledge of ant–symbiont interactions on other continents is extremely fragmentary and poorly understood. Moreover myriad unknown symbionts presumably await discovery and description in these continents (Parmentier, 2020). By contrast, a firm body of knowledge on the distribution and diversity of ant symbionts in Europe has been recorded and has grown steadily from a long tradition of studying ant symbionts since the end of the 19th century (Wasmann, 1894; Janet, 1897). We focused on all types of macrosymbionts (multicellular organisms) associated with European ants. We did not include microsymbionts (unicellular microorganisms such as bacteria), as only a few case studies are available. In addition, these symbionts differ completely in their strategies and dynamics. Depending on the intimacy of the relationship between ants and symbionts, we can distinguish obligate and facultative interactions. An obligate interaction occurs when a symbiont lives permanently inside or near an ant nest. Obligate symbionts depend completely on ants and cannot be found without them. Facultative myrmecophiles may associate with ants, but regularly (or mostly) occur without ants. This study focuses on obligate symbionts. We categorized five types of symbionts: (1) myrmecophiles; (2) trophobionts; (3) social parasites; (4) helminths; and (5) fungi (Table 1). Myrmecophiles were further subdivided into three functional groups: unspecialized myrmecophiles, specialized myrmecophiles and myrmecophilous parasitoids (Table 1).

Plants engaging in mutualistic relationships (e.g. myrmecochory) were not included in our analyses. Contrary to the tropics, ant–plant relationships tend to be loose in Europe and are at best facultative (Rico-Gray & Oliveira, 2007).

(2) Ant–symbiont data set compilation

We compiled documented ant–symbiont interactions in Europe. Our database of ant–symbiont interactions was assembled from 269 published references, including faunistic notes, research articles, reviews and books. In a first round of searches, we scanned reference works (e.g. Wasmann, 1894; Donisthorpe, 1927; Evans & Till, 1966; Uppstrom, 2010; Tykarski, 2017; Molero-Baltanás *et al*. 2017) for associations between ant hosts and symbionts. Next, we searched for ant–symbiont interactions *via Google Scholar* using the terms: "myrmecophile" or "ant associate" or "inquiline" or "ant guest" or "ant symbiont". We also found host–symbiont interactions within the reference lists of the retrieved publications. In a second phase, each symbiont occurring in Europe was searched by its Latin binomial name and its common taxonomic synonyms combined with a search string with the names of all ant genera (N = 56; AntWiki, 2019) found in Europe (for example "*Phengaris alcon*" AND *Acropyga* OR *Anochetus* OR *Aphaenogaster* OR *Bothriomyrmex* OR *Camponotus* OR …) using *Google Scholar*. We chose *Google Scholar* over ISI Web of Science, as the latter does not retrieve faunistic notes or other types of grey literature. We omitted symbionts from our data set when they were reported not to be associated with ants. Note that some species with a poorly studied biology, such as parasitoid wasps and mites, were included in our data set, although they may not be completely dependent on ants. Ultimately, we obtained a binary host–symbiont matrix (see online Supporting information Appendix S1, references used to compile this table are listed in Appendix S2) filled with interactions (1) and non-interactions (0) between ants (columns) and symbionts (rows). We included some references on ant–

trophobiont interactions reported in the non-European part of Russia (e.g. Novgorodova, 2005) to increase the relatively modest number of reported interactions in this type of association. The reported ants and trophobionts in these references have a widespread Palearctic distribution and they are expected to interact in Europe as well.

(3) Host specificity in different symbiont types

We first determined the host range of the different symbiont types. A second analysis compared host relatedness across symbiont types. We used two approaches to estimate host relatedness: taxonomic and phylogenetic relatedness.

In the first analysis, we compared the number of host species across seven different types of host symbionts, i.e. unspecialized myrmecophiles, specialized myrmecophiles, myrmecophilous parasitoids, trophobionts, social parasites, parasitic fungi and helminths (Table 1). Symbionts with hosts only identified at the genus level were not included in all subsequent analyses. Note that we found evidence of one mutualistic fungus (*Cladosporium myrmecophilum*) (Table 1), but we only analysed parasitic fungi to ensure a coherent functional group of symbionts. Studies are uneven across symbionts, potentially meaning that better studied symbionts have a higher number of recorded host species. To account for differences in sampling effort, we therefore first performed a regression of the total number of host species against the (ln+1)-transformed number of *Google Scholar* hits for the binomial species name (and commonly used synonyms) of the symbionts. The residuals of this regression were not normally distributed. Therefore we used a non-parametric Kruskal-Wallis test to compare these residuals across symbiont types. This test was followed by *post-hoc* Dunn tests with the Benjamini–Hochberg adjustment for multiple testing.

In the second analysis, we compared the relatedness of targeted host species across the seven different symbiont types. For each symbiont, we estimated the average taxonomic distance

between the different hosts by using the specificity index, S_{TD} proposed by Poulin & Mouillot (2003). Host ant species (all ants belong to the family Formicidae) were classified following Linnaean classification into subfamilies, tribes, genera and species groups/subgenera. The taxonomic distance between two hosts is then defined as the number of hierarchical steps that are needed to reach a common node in the taxonomic tree. The taxonomic distance between two species of the same subgenus/species group equals 1; the distance between two species of the same genus, but from a different subgenus/species group equals 2. A distance of 3 or 4 was assigned to a pair of species belonging to the same tribe or subfamily, respectively. A taxonomic distance of 5 is reached between two ant host species from different subfamilies (largest possible distance). S_{TD} was estimated by averaging the taxonomic distance across all pairs of host species. However, S_{TD} cannot be calculated for symbionts with a single host species, although this can be addressed by excluding these 'singletons' from the analyses (Poulin & Mouillot, 2005). The single host species for many of our symbionts (e.g. mites) likely reflects undersampling, rather than true specificity to a single host species, because even extremely specialized species (e.g. *Microdon*, *Claviger*, social parasites) often have more than one host species. Since these singletons were equally distributed over all groups of symbionts, we argue they could be omitted from further analyses; a total of 392 symbionts were retained in our analysis. Note that the S_{TD} is not affected by uneven sampling when dealt with in this way. We modelled the S_{TD} as a response variable against the predictor symbiont type with a non-parametric Kruskal-Wallis test, followed by *post-hoc* Dunn tests with the Benjamini–Hochberg adjustment for multiple testing. Alternatively, we can assign a default taxonomic distance of 1 to the singletons, which is the lowest possible value (Poulin & Mouillot, 2005). We repeated the analysis with this approach and compared it with the analysis without singletons.

Next, we compared the relatedness of the targeted host species across the symbiont types with a phylogenetic- instead of a taxonomic-distance matrix. The phylogenetic-distance matrix was based on the phylogenetic tree of European ants (Arnan, Cerdá & Retana, 2017). Distances between species were estimated by node count (number of nodes along the branches of the tree from one species to another) and were retrieved using Mesquite v.3.5. Phylogenetic distances are more accurate than taxonomic distances to assess relatedness, but unfortunately we do not possess phylogenetic information at the species level for all ants in our data set (the phylogeny was known for 108 out of 181 ant species). We decided to exclude the 73 ant species without phylogenetic information and their interactions with their symbionts from subsequent analyses. We believe that this is acceptable as the retained 108 species cover 87.8% of the interactions in our host species–symbiont data set. In addition, symbionts that interacted with only one ant species were omitted, as no specificity index could be calculated for these species. Ultimately, we retained 362 symbiont species and 108 ant species in this analysis (host–symbiont matrix in Appendix S3). As the residuals meet the assumptions of a general linear model (GLM), we ran a GLM using phylogenetic distance as the response variable and symbiont type as predictor. Significance of the model was assessed with a likelihood ratio test (ANOVA function implemented in the package car), pairwise *post-hoc* tests were conducted with the Benjamini–Hochberg adjustment for multiple testing.

(4) Predictors of symbiont diversity in European ants

A central question in this study is why some ant species host more symbionts than other ant species. Therefore, we first compiled for the European ant species several predictors based on Arnan *et al.* (2017), Boulay *et al.* (2017), Seifert (2007) and AntWiki (2019). We selected traits of the host that could affect symbiont diversity. These predictors were colony size (number of workers), average worker size (mm), nest type [levels: (*a*) arboricolous; (*b*)

diverse; (*c*) soil; and (*d*) organic mound] and phylogeny as a proxy for trait similarity, and factors reflecting differences in the functional role of the host species, including habitat [levels: (*a*) eurytope: – a broad range of niches, including anthropogenic habitats; (*b*) open; (*c*) open/sylvicolous; and (*d*) sylvicolous], distribution range, the number of sympatric ants and biogeographic region [levels: (*a*) atlantic; (*b*) boreo-mountain; (*c*) continental; (*d*) Mediterranean; and (*e*) wide-ranging]. Ants were assigned to the biogeographical region where they were found proportionally the most in sampled biogeographical regions based on the observations of Arnan *et al.* (2017). If the proportional occurrence in the most preferred region was less than double the proportional occurrence in another region, the ant species was grouped under the 'wide-ranging' category. We also estimated the distribution range [the number of countries where the host species has been reported, based on records on AntWiki (2019)], the number of sympatric ants [number of ant species with symbionts which share at least one country in the distribution range, based on AntWiki (2019)] and the number of hits for their binomial name (and common synonyms) on *Google Scholar* as a proxy for sample effort for every ant species. Next we correlated total symbiont diversity with the host predictors described above, while correcting for the phylogenetic relatedness of the different ant species. The phylogenetic relatedness of host species should be accounted for as closely related host species cannot be treated as independent observations. For that reason, we modelled a phylogenetic generalized least-squares regression (PGLS) with total number of symbionts per ant species as the dependent variable. A PGLS model incorporates a phylogenetic variance–covariance matrix in its error structure. We used the variance–covariance matrix based on the pairwise node counts retrieved from the phylogenetic tree of European ants by Arnan *et al.* (2017). The phylogenetic relatedness of 108 out of the 181 ant species found in our data set was determined in this tree (see Appendix S3). From this subset of 108 species, we were able to find values for all predictors for 96 species. Consequently, the

PGLS model was based on these 96 ant species (Appendix S4). This data set reduction is acceptable as these 96 ant species interact with 620 symbionts and cover 86.5% of the recorded interactions in the host species–symbiont data set. The phylogenetic covariance matrix was multiplied by Pagel's λ, a widely used parameter that scales and corrects for the expected degree of phylogenetic covariance (Pagel, 1999). This multiplier spans from 0, which corresponds to the complete absence of a phylogenetic signal in the residuals of the model (the model is then similar to a regular GLM with an ordinary least-squares error structure) to 1, when the covariance of the model residuals follows a Brownian motion model of evolution (Pagel, 1999; Freckleton, Harvey, & Pagel, 2002). The λ parameter characterizing the phylogenetic signal was estimated through maximum likelihood estimation within the PGLS model. We analysed this model using the *pgls* function embedded in the R 3.5.1-package 'caper'. We transformed the variables to meet the normality assumptions of the residuals. Number of symbionts was square–root transformed, the predictors colony size, the number of sympatric ants and *Google Scholar* hits ln-transformed, and the distribution range was square-root transformed. Finally, all continuous predictors were scaled to unit variance. In addition to this analysis on the drivers of total symbiont diversity, we ran similar PGLS models with subsets of symbiont species richness as dependent variables (overall number of myrmecophiles, trophobionts, social parasites and helminths, separately) and predictors of the subset of ant species that engage with these symbionts as predictors. Identical transformations of predictors and subsets of symbiont richness were applied as in the analysis on total symbiont richness described above. Diversity of fungi was not regressed against ant predictors in separate PGLS models as the number of host ants is relatively low in these groups. Models were ranked per analysis with the *dredge* function in the 'MuMIn' R-package according to their corrected Akaike Information Criterion (AICc) value. We retained the best

models identified with ΔAICc < 2. Significance levels of the predictors of the retained models were assessed using Wald χ^2 tests.

(5) Predictors of symbiont sharing in European ants

Studying the factors that facilitate or constrain the transmission of a symbiont from one host to another is pivotal to understanding the ecological and co-evolutionary processes in host–symbiont networks (Okuyama & Holland, 2008; Pilosof *et al*., 2013). For example, symbionts that are only shared by closely related hosts may indicate host–symbiont co-evolution in the network (Guimarães, Jordano & Thompson, 2011). Predictors were similar to the previous analysis and encompassed traits of the ant species and variables related to their habitat and distribution, including colony size, worker size, nest type, phylogeny as a proxy for trait similarity, habitat, distribution range, biogeographic region and allopatric distribution. We used multiple regression on distance matrices (MRM), an extension of partial Mantel analysis, to test the association between different distance matrices (Lichstein, 2007). The symbiont dissimilarity matrix contained the pairwise Jaccard distances between each pair of host ants based on the presence–absence data of the symbionts they supported. This matrix was regressed against multiple distance/dissimilarity matrices giving dissimilarities in the aforementioned predictors. Worker size difference was the absolute difference for this trait between every pair of ant species. The pairwise differences in colony size were ln-transformed. For the allopatric distribution matrix, we first calculated the degree of overlap in distribution (sympatry) between each pair of species (ln-transformed number of countries in the distribution range that are shared between each pair of ant species). We standardized this matrix between 0 and 1 and subtracted it from 1 to obtain a dissimilarity matrix. Entries in the distance matrices of habitat, nest type and biogeographic region were coded 0 when the pair of ants occupy the same habitat, nest type or biogeographic region, respectively, and 1 when

the pair of ants show differences in these variables. The phylogenetic distances were the pairwise node counts. Again, we focused our analysis on the subset of 96 ants for which the phylogenetic relationship was resolved by Arnan *et al.* (2017) and for which we possessed values for all predictors. We also included a matrix of sampling effort in which we pairwise multiplied the (ln+1)-transformed hits on *Google Scholar* of one ant species with the (ln+1)-transformed hits on *Google Scholar* of another ant species. All matrices were standardized between 0 and 1 and MRM analyses were conducted in the R package 'ecodist' using the MRM function. Significance of the predictor matrices was tested using 9999 permutations. We removed non-significant predictors, and reran the MRM analysis until all predictors were significant (Martiny *et al.*, 2011). The relative importance of the significant predictor matrices was calculated with the lmg metric, which uses unweighted averages of sequential R^2 of different orderings of the model predictors. The calculation and visualization of the lmg metrics was conducted with the R-package 'relaimpo'.

We conducted similar MRM analyses on subsets of the symbiont community, where the response variable was the dissimilarity (pairwise Jaccard indices) in the set of myrmecophiles, trophobionts, social parasites, helminths and parasitic fungi of the host ants, respectively.

All statistical tests were conducted in R 3.5.2.

III. RESULTS

(1) Ant–symbiont networks display a diversity of species interactions

We identified 722 obligate ant symbionts interacting with 181 ant species in Europe (Appendix S1). The references we used to compile the host–symbiont interaction matrix are listed per symbiont species in Appendix S2. Myrmecophiles (N = 535) outnumbered the four other types of ant symbionts (N = 80, N = 71, N = 22 and N = 14 for trophobionts, social parasites, parasitic helminths and fungi, respectively). One fungus was mutualistic, the other

13 species were parasitic. Within the group of myrmecophiles, beetles and mites were the most species-rich groups (Fig. 1). The subdivision of myrmecophiles into parasitoids (N = 33), unspecialized myrmecophiles (N = 413) and specialized myrmecophiles (N = 89) can be found in Appendix S1. The hosts of 75 symbionts were not identified at the species level in the literature record. The distribution of the number of host species per symbiont was right-skewed (mean = 3.58, median = 2). The highest frequency (39%) of symbionts interacted with one host species and a maximum number of 34 host species was documented in the myrmecophilous silverfish *Proatelurina pseudolepisma*.

European ant genera contained a highly variable number of species (proportional to the genus font size in Fig. 2; Fig. S1), ranging from 1 to 82, in the genera that interact with symbionts. Generally, the species-rich ant genera, such as the Formicinae genera *Lasius*, *Formica* and *Camponotus* and the Myrmicinae genera *Messor* and *Myrmica* attracted a higher diversity of all five types of symbionts (Pearson's product-moment correlation: $r = 0.59$, $P < 0.001$, d.f. = 30; Fig. S1). A notable exception was the European ant genus *Temnothorax*, which contained the most species while supporting a relatively moderate number of symbionts. Myrmecophiles were the dominant group in most ant genera. Trophobionts were generally the second most diverse group, but were absent or nearly absent in some genera such as *Monomorium*, *Aphaenogaster, Leptothorax, Messor, Temnothorax* and *Cataglyphis*. Social parasites contributed slightly to total symbiont diversity in most ant genera, but were very diverse in the ant genera *Temnothorax*, *Tetramorium* and *Leptothorax*. Helminths and fungi represent a minor fraction of the symbiont fauna in almost all ant genera. However, fungi are well-represented in *Myrmica*. Ant genera shared many symbionts with other genera (78.9% of the hosted community on average), belonging to the same or different ant subfamilies (connecting lines in Fig. 2). *Temnothorax*, *Leptothorax* and *Messor* are characterized by a relatively high number of unique symbionts (see relatively large inner circles in Fig. 2).

447

448 **(2) Host specificity in different symbiont types**

449 After controlling for sampling effort, symbiont groups had significantly different host ranges
450 (Kruskal-Wallis chi-squared = 44.97, d.f. = 6, $P < 0.001$; Fig. 3). Social parasites had the
451 lowest number of host species (Fig. 3, *post-hoc* comparisons indicated with letter code). Other
452 symbiont types interacted with a higher number of ants, but we did not detect significant
453 differences among these other types (Fig. 3). Host range of symbiont groups without
454 controlling for sampling effort can be found in Fig. S2.
455 The average taxonomic distance between host species targeted by a symbiont was
456 significantly different among symbiont groups (Kruskal-Wallis chi-squared = 83.37, d.f. = 6 ,
457 $P < 0.001$; Fig. S3). The approach where we omitted the symbionts with one host species
458 (Fig. S3) and that where we assigned a taxonomic distance of 1 to these species (Fig. S4)
459 provided similar results (relative differences among symbiont groups are very similar in Figs
460 S3 and S4). Likewise, we found significant differences in average phylogenetic distance
461 between host species across the symbiont groups (GLM, $F = 17.27$, d.f. = 6, $P < 0.001$; Fig.
462 4). Patterns in the average host phylogenetic distance of the different symbiont groups closely
463 matched those of the average host taxonomic distance. Host species of social parasites were
464 very closely related to each other (Figs 4 and S3). Parasitic fungi also exploited related host
465 species. Helminths and myrmecophiles interacted with hosts that are much more unrelated on
466 average. We did not find differences in host relatedness among myrmecophilous parasitoids,
467 unspecialized and specialized myrmecophiles (Figs 4 and S3). Ants interacting with
468 trophobionts showed the lowest relatedness (Fig. 4).
469

470 **(3) Predictors of symbiont diversity in European ants**

The number of symbionts is highly variable in ant species. Here we report the host drivers that affect total symbiont richness and diversity of four subsets of ant symbionts (myrmecophiles, trophobionts, social parasites and helminths). Total symbiont diversity was clearly positively correlated with colony size. This factor was highly significant (PGLS, $P < 0.001$) in the four top-ranking models (Table 2, Fig. 5). Habitat and distribution range of the host were also incorporated in most of the top-ranking models. In these models, symbiont richness increased with the host distribution range and was highest in eurytopic habitats (PGLS, $P < 0.001$). As expected, sample effort has a major effect on the reported total symbiont diversity and the other subsets of symbiont diversity. Symbiont interactions were highest in ants that are intensively studied. We controlled for sample effort by including the proxy (ln+1)-transformed *Google Scholar* hits in our models. Myrmecophile richness was also positively affected by colony size (PGLS, $P < 0.001$ in the five top-ranking models, Table 2, Fig. 5), distribution and eurytopic habitat. Myrmecophiles were more abundant in larger ants (PGLS, $P < 0.05$ in the retained models). Trophobiont diversity was positively correlated with sampling effort and an eurytopic habitat in most models (Fig. 5, Table 2). Trophobiont diversity was in some models also higher in ant species with a higher distribution. There were no predictors consistently present in the top-ranking models explaining social parasite species richness (Table 2) Helminth diversity was higher in eurytopic ant species, but no other predictors were consistently retained in the top models (PGLS, $P < 0.001$, Table 2).

We found a phylogenetic signal in the predictors of the PGLS models (Δ AICc < 2) with total symbiont richness as dependent variable (Pagel λ ranged from 0.41 to 0.54 Table 2). The residuals of the models showed different degrees of phylogenetic covariance. The largest phylogenetic signal was found in the models with social parasites (Pagel λ ranged from 0.83 to 1.00) and helminths (Pagel λ ranged from 0.85 to 0.94) as dependent variable. By contrast,

phylogenetic relatedness of the hosts did not explain additional variation (Pagel's $\lambda = 0$) in most retained models with myrmecophiles as dependent variable (Table 2).

(4) Predictors of symbiont sharing in European ants

The dissimilarity matrices of the host predictors (indicated with Δ in Fig. 6) were positively correlated with dissimilarity in symbiont composition (Fig. 6). This shows that ant species with a higher similarity in these predictors display a higher similarity in symbiont composition. The most important predictors of similarity in ant symbiont communities in the European ant data set were phylogenetic relatedness of the ant hosts (MRM, lmg = 0.40, $P < 0.001$) and similarity in biogeographic region (MRM, proportional contribution to the total r^2 = lmg = 0.35, $P < 0.001$) (Fig. 6). Similarities in worker size (lmg = 0.07, $P = 0.01$), colony size (lmg = 0.04, $P = 0.02$) and habitat (lmg = 0.01; $P = 0.03$) also facilitated the sharing of symbionts (Fig. 6). Better studied ant pairs shared more similar symbiont communities (MRM, lmg = 0.13, $P < 0.001$). Well-studied ant pairs also shared more trophobionts, myrmecophiles and parasitic fungi (MRM-analyses, lmg ranging from 0.14-0.60, all $P < 0.05$, Fig. 6). Trophobiont sharing was also positively correlated with phylogenetic relatedness and similarity in biogeographic regions of the ant hosts (MRM, lmg = 0.22, $P < 0.001$ and lmg = 0.13, $P < 0.001$, respectively). The similarities in social parasite communities was largely explained by phylogenetic relatedness (MRM, lmg = 0.76, $P < 0.001$). Similarities in biogeography (MRM, lmg = 0.04, $P = 0.04$) explained additional variation in the sharing of social parasites. Helminth sharing was also strongly facilitated in phylogenetically related ant hosts (MRM, lmg = 0.71, $P < 0.001$). Interestingly, phylogenetic relatedness of the hosts did not promote the sharing of myrmecophiles. The similarity of myrmecophile communities between ant hosts was mainly driven by living in a similar biogeographic region (MRM, lmg

519 = 0.68, $P < 0.001$), Lastly, ants in the same biogeographic region tend to share more parasitic
520 fungi (MRM, lmg = 0.44, $P < 0.01$) (Fig. 6).
521
522 **IV. DISCUSSION**
523 Understanding community composition and stability is an important challenge in ecology.
524 Network analysis has approached this challenge, using community structure and species
525 interactions as fundamental building blocks. Yet, studies that explain the detailed topology of
526 large-scale ecological networks encompassing a diversity of interaction types are limited. We
527 here provide a complete tally of the distribution of ant symbiont groups over European ants
528 and compare host specificity, symbiont richness, host switching and its drivers for different
529 ant symbiont groups.
530
531 **(1) Characterization of the European ant–symbiont network**
532 It is widely acknowledged that the group of obligate ant symbionts is hyperdiverse
533 (Wasmann, 1894; Kistner, 1979, 1982; Hölldobler & Wilson, 1990; Rettenmeyer *et al.*, 2010),
534 although exact species numbers at a regional scale are lacking. Rough estimates of the global
535 diversity of parasites living in ant nests reach 10,000 to 20,000 species (Thomas, Schönrogge
536 & Elmes, 2005), which is higher than mammal and bird diversity. We here identified 722
537 symbionts distributed over 181 ant species in Europe. The majority of these symbionts were
538 classified as myrmecophiles, which are commensalistic-to-parasitic arthropods mostly living
539 inside the ant nest (Kronauer & Pierce, 2011; Parmentier *et al.*, 2016*a*; Parmentier, 2020).
540 Beetle and mite communities were the most diverse groups. In other regions, beetles and
541 mites also outnumber other myrmecophilous arthropod groups (Kistner, 1982; Hölldobler &
542 Wilson, 1990). Social parasites and mutualistic trophobionts are medium-sized groups;
543 endoparasitic helminths and parasitic fungi are relatively species-poor, but understudied.

544 Mutualistic ant symbionts are thus clearly overshadowed by the diversity of commensalistic
545 and parasitic ant symbionts in Europe. Species-rich ant genera and subfamilies generally
546 supported higher numbers of ant symbionts. Host–symbiont networks are characterized by an
547 asymmetrical organization of interactions with host-specific symbionts and symbionts that
548 interact with multiple host taxa (Guimarães *et al.*, 2006). Overall, a large proportion of the
549 symbionts were shared among heterogeneric ant species (Fig. 2). Some ant genera interacted
550 with a relatively low number of symbionts, but most of their symbionts were not found in
551 association with other ant genera. The highly specific group of social parasites was much
552 more represented in the symbiont community of these hosts. In addition, the group of
553 trophobionts is diverse in some ant genera, but is marginal or even absent in others (Fig. 2).
554 The distribution of trophobiont interactions across the ant genera echoed the dietary
555 preferences of the host. The diet of genera such as *Formica*, *Lasius* and *Myrmica* consists of a
556 significant proportion of honeydew, whereas genera with few or no trophobiotic interactions
557 are known to be predatory (e.g. *Temnothorax*, *Cataglyphis*) or granivorous (e.g. *Messor*)
558 (Seifert, 2007). Mutualistic interactions are much more diverse in tropical systems than those
559 observed in the European network and include ant-cultivated plants, ant-defended plants and
560 ant-cultivated fungi (Rico-Gray & Oliveira, 2007). The uneven distribution of the five types
561 of symbionts among the European ant genera suggests that some ant lineages are more
562 predisposed to associate with particular types of symbionts. Ant–host associations are thus
563 shaped by deep evolutionary processes as determined by biotic and environmental drivers of
564 speciation and extinction (Aguilée *et al.*, 2018).
565
566 **(2) Host specificity in different symbiont types**
567 Host specificity is a key feature of host–symbiont networks, and is moulded by the ecological
568 and evolutionary interactions between the host and symbiont (Poulin & Mouillot, 2003).

569 Patterns in host specificity have been studied in a wide range of host–symbiont systems.
570 Generally, parasites are thought to have a tendency to evolve to extreme host specialization as
571 they need complex adaptations to bypass host defences (Kawakita *et al.*, 2010). The drivers
572 favouring host specificity in mutualist partners are far less understood and both low and high
573 degrees of specificity are widespread (e.g. plant–seed dispersers and fig–fig wasps,
574 respectively). Ant symbioses are ideal to unravel patterns in host specificity. They occupy the
575 complete mutualism–parasitism continuum and allow comparison of host specificity in
576 different types of symbionts. We here demonstrate that average host range in European ant
577 symbionts was much broader than previously assessed in a study on host specificity of
578 myrmecophiles at a global scale (Glasier *et al.*, 2018) which found that obligate ant symbionts
579 occurred on average with *ca*. 1.20 host species. We, however, found that European symbionts
580 were reported with three times this number of host species (3.58) on average. The much lower
581 number of detected hosts in Glasier *et al.* (2018) is probably the result of their searching
582 method. They did not include data from faunistic notes, grey literature and books, which
583 report the majority of interactions between ants and their symbionts. Moreover, the symbiont
584 fauna, let alone the range of their interactions, is poorly documented outside Europe, which
585 makes hard predictions at a global scale unreliable (Parmentier, 2020). Ant symbionts were
586 extremely variable over the host-ant range. After controlling for sampling effort, social
587 parasites clearly targeted the lowest number of host species, which is in line with expectations
588 as they are the most specialized group of parasites (Buschinger, 2009). Apart from the number
589 of hosts, the relatedness of host species is also a vital aspect of host specificity. It is well
590 described that social parasites colonize nests of related hosts (Emery's rule; Buschinger,
591 2009). However, this has not been compared with other types of symbiont groups. We showed
592 that the hosts of social parasites were clearly the most related of all symbiont types. The hosts

of myrmecophiles, parasitic fungi and helminths showed moderate to poor relatedness on average. Trophobionts were associated with the most distantly related ant species.

There is a large body of literature that explains the constraints of host switching in social insect symbionts. Generally, it is thought that specialized myrmecophiles and social parasites rely on chemical deception, by mimicking the colony recognition cues or some key pheromones (overview in Parmentier, Dekoninck & Wenseleers, 2017). They are completely integrated into the host colony and are treated as a true colony member. Because of this strict mimicking of the host's communication system, they are not able to colonize unrelated host species. Unspecialized myrmecophiles are typically poorly integrated into the colony, but host switching is more common in this group. This is facilitated by the use of general defensive chemicals, chemical insignificance or behavioural strategies (Stoeffler, Tolasch & Steidle, 2011; Parmentier *et al*., 2017, 2018). Consequently, we predicted that specialized myrmecophiles would display much higher degrees of host specificity than unspecialized myrmecophiles. Surprisingly, we did not find differences in the number of host species and host relatedness among unspecialized myrmecophiles, specialized myrmecophiles and parasitoids. A limitation of the present study is that we do not have information on the relative importance of the recorded host species for a symbiont. It is likely that some of the listed host species of specialized symbionts rarely act as hosts, resulting in an overestimation of the actual species range and host species relatedness of symbionts. Additionally, the biology of most myrmecophiles is poorly known, which makes a functional grouping according to specialization challenging and open for refinement. The processes which make trophobionts attractive to one host, but not to another are hitherto unexplored. Likewise, the mechanisms of host switching and the factors that facilitate or constrain host switching in endoparasitic helminths and fungi are unknown.

(3) Predictors of symbiont diversity in European ants

Associations between ant hosts and their symbionts are not random and are structured according to both ecological and evolutionary factors that act at different spatiotemporal scales. From the perspective of ant symbionts, ant nests can be conceptualized as habitat islands. Ant species with larger ant nests interact with more symbiont species. Nest size of ant species has been repeatedly hypothesized as an important driver of ant symbiont diversity (Hughes, Pierce & Boomsma, 2008; Kronauer & Pierce, 2011), and here was formally tested for the first time. Previous studies across very different host–symbiont systems [e.g. ectoparasites of fishes (Guégan *et al*., 1992), parasites of hoofed mammals (Ezenwa *et al*., 2006), parasites of carnivores (Lindenfors *et al*., 2007), feather mites of finches (Villa *et al*., 2013)] identified the size of the host species as one of the key factors in determining symbiont species richness (Kamiya *et al*., 2014). This positive association results from the fact that larger host species provide more niches and are less ephemeral (Lindenfors *et al*., 2007). Analogously, ant species with larger nests provide more space to allow larger population sizes, thereby reducing the extinction risk of symbionts (*cf.* island theory; Macarthur & Wilson, 1967). In addition, ant species with larger nests provide a higher diversity of microhabitats, including refuge areas that eventually facilitate species coexistence (Barabás *et al.*, 2018). Larger ant nests are also expected to be more persistent (Kaspari & Vargo, 1995). The colony size of ant species is thus a strong local driver of total symbiont richness, and myrmecophile richness in particular.

Total symbiont diversity, myrmecophile diversity, helminth and trophobiont diversity are additionally determined by more regional ecological factors like range size and niche width of the host ants. In that respect, eurytopic ants, such as *Lasius niger* and *Myrmica rubra* that can live in a wide variety of habitats including urban regions, hosted more symbionts, myrmecophiles, trophobionts and helminths. An effect of both distribution and habitat reflects

643 that more symbionts occur in widely distributed ant species with high densities. Symbionts
644 associated with widely distributed ants are less prone to extinction as predicted by life-history
645 theory and metacommunity ecology (Nosil, 2002; Leibold *et al*., 2004).
646 Host density has widely been demonstrated as a key factor explaining parasite species
647 richness (Lindenfors *et al*., 2007). Interestingly, we found that species with larger workers
648 engaged with more myrmecophiles than ant species with small workers. This pattern in
649 myrmecophile diversity was previously hypothesized based on experimental work, showing
650 that the survival of three myrmecophilous beetles gradually increased in laboratory nests of
651 larger ant species (Parmentier, Dekoninck & Wenseleers, 2016*b*). This positive relationship
652 between ant size and myrmecophile diversity suggests that species with small workers detect,
653 attack and deter myrmecophiles more easily and efficiently.
654 Sampling effects appear highly relevant in most models of symbiont diversity among different
655 hosts. Trophobiotic and more specialized parasitic interactions as seen in the group of
656 helminths and social parasites are more determined by evolutionary drivers than
657 myrmecophiles. Indeed, affinity with their hosts is strongly shaped by the phylogeny of the
658 host. The effect of phylogeny is echoed in the high Pagel's lambda values of the
659 corresponding PGLS models, implying that much of the residual variation in trophobiont and
660 especially helminth and social parasite richness could be explained by the phylogeny of the
661 hosts. This strong phylogenetic driver for social parasite richness is in line with our previous
662 results that social parasites mainly target closely related ant species (referred to as Emery's
663 rule; Buschinger, 2009) belonging to a small number of ant genera. Symbiont network
664 structure thus shifts from more neutral ecological drivers related to regional species
665 abundance to co-evolutionary drivers related to ancestry. The uniqueness and tightness of
666 species interactions are known to be both a driver and consequence of co-evolutionary
667 dynamics. Interestingly, we here show that these evolutionary drivers overrule any ecological

668 one in the most specialized interactions (social parasites), hence demonstrating the integrated
669 nature of symbiont network formation according to the prevailing interaction strengths. Other
670 predictors, which were not considered in the analyses, may also positively affect the diversity
671 of symbionts. The availability of larvae and pupae rather than colony size may be more
672 important for parasitoid species (Rocha *et al.*, 2020). The tolerance level of ant species to
673 intruders and the colonial organization (either single nests or multiple connected nests, either
674 a single queen or multiple queens) are also possible determinants of diversity, but sufficient
675 information is lacking to test these hypotheses.
676 Ant–symbiont networks are unique in the sense that the host-associated network that is
677 studied covers a wide array of interactions, from putatively mutualist to strictly antagonistic.
678 We found that evolutionary processes are pivotal in networks of the most specialized ant
679 symbionts (social parasites), whereas less-specialized networks, as found in the group of
680 myrmecophiles, were mostly determined by ecological factors. The same pattern was found in
681 other symbiont systems. Studies on specialized host–parasite networks equally point at the
682 dominance of evolutionary drivers (phylogeny and biogeography) of these associations (Feliu
683 *et al.*, 1997; Rosas-Valdez & de Pérez-Ponce de León, 2011), while less-obligatory animal
684 parasitic (Nunn *et al.*, 2003; Ezenwa *et al.*, 2006; Lindenfors *et al.*, 2007; Nava &
685 Guglielmone, 2013) or plant mutualistic interactions (Sanders, 2003; Wagner, Mendieta-
686 Leiva, & Zotz, 2015) are more affected by ecological factors related to distribution and
687 abundance patterns that enhance contact and hence transmission of their diversity and host-
688 association patterns.
689
690 **(4) Predictors of symbiont sharing in European ants**
691 We hypothesized that the shared evolutionary history of related ant species would promote the
692 sharing of similar symbiont communities. A positive correlation between phylogenetic

693 relatedness of the hosts and symbiont sharing was demonstrated in previous studies on orchid
694 mycorrhiza (Jacquemyn *et al.*, 2011) and bat viruses (Luis *et al.*, 2015), but no such
695 relationship was found in arbuscular mycorrhiza (Veresoglou & Rillig, 2014) and primate
696 parasites (Cooper *et al.*, 2012). Consistent with our prediction, we found that the main factor
697 that promoted symbiont sharing in European ants was the relatedness of the hosts. It indicates
698 that many symbionts pass more easily to related host species. As related ant species employ
699 nearly identical defence structures (nestmate recognition cues, physiological and behavioural
700 defences), it enables symbionts, especially specialized parasites, to bypass the host defence
701 systems of related hosts. Another key factor that may facilitate the cross-species transmission
702 of symbionts is the overlap in geographical distribution of the hosts (*cf.* bat viruses in Luis *et*
703 *al.*, 2015). We showed that ant species living in the same biogeographical region possessed
704 more similar symbiont communities. This suggests that both the spatial overlap and similarity
705 in climatic conditions facilitate the sharing of symbionts. Sampling effort also considerably
706 explained the sharing of symbionts. More shared symbionts were reported in well-studied
707 pairs of species. Focusing on the different subsets of ant symbionts, we found that the sharing
708 of trophobionts between host ant species was mainly determined by biogeography and
709 phylogenetic relatedness. Phylogenetic relatedness of the hosts was the most important driver
710 explaining the sharing of helminths and social parasites. The strong phylogenetic effect on the
711 sharing of social parasites is directly linked to the very low taxonomic/phylogenetic distance
712 between their hosts. Social parasites target a very narrow range of host species by hijacking
713 their communication system. This exploitation of host cues is facilitated by immediate
714 common ancestry (Buschinger, 2009). The biology of most helminths is unknown, but
715 probably immune evasion is only possible in related host species. Myrmecophiles and
716 parasitic fungi were more similar in ant species residing in the same biogeographical region.
717 Climatic conditions have a strong effect on the distribution of different groups of

718 myrmecophiles. One example is the large group of myrmecophilous silverfish which are
719 mainly confined to ants living in the Mediterranean region (Molero-Baltanás *et al*. 2017;
720 Appendix S1). Interestingly, host switching of myrmecophiles and parasitic fungi was not
721 positively correlated with host relatedness (*cf.* Cooper *et al.*, 2012; Veresoglou & Rillig,
722 2014).
723
724 **V. OUTSTANDING QUESTIONS**
725 Merging different interaction types into one ecological network framework is a key challenge
726 in ecology (Fontaine *et al*., 2011). Diverse host–symbiont communities provide an
727 opportunity to test the relative contributions of ecology and evolution to network assembly.
728 For example, our study on ant–symbiont networks revealed different roles of ecological and
729 evolutionary processes depending on the type of symbiosis. Our insights may provide a basis
730 for theory development and across-ecosystem comparisons (e.g. plant- and coral-based
731 networks) and synthesis.
732 We lack theory on how the architecture and the interaction signs and sizes jointly affect the
733 stability and productivity of these diverse networks, much in contrast to trophic or mutualistic
734 networks. The relative ease with which one can manipulate ant–symbiont communities makes
735 them suited as empirical systems to test theory.
736 Host–symbiont networks offer an opportunity to understand both ecological and evolutionary
737 processes behind community assembly, from meso- to macro-ecological scales (see Vellend,
738 2016). More specifically, as hosts occur spatially structured at these scales, it remains an open
739 question how these assembly processes are determined by ecological and evolutionary
740 limitation of dispersal. One key question is whether and how symbionts are dispersing: to
741 what degree is horizontal transfer and subsequent symbiont sharing across hosts a facilitator
742 of symbiont community assembly, and to which degree is vertical transfer, i.e. co-dispersal of

743 symbiont and host, established across the antagonism–mutualism gradient of host–symbiont
744 networks? Mutualistic plant mycorrhizal fungi and plant diaspores, for instance, are passively
745 co-dispersed by birds (Correia *et al.*, 2019). Are similar processes equally prevalent in ant–
746 symbiont interactions, for instance are symbionts transported by their host during colony
747 relocation (Parmentier, 2019)?
748 Empirical data demonstrate that different host ants coexist regionally. The stabilizing and
749 equalizing mechanisms that underpin such coexistence are at present unknown. How do the
750 complex symbiont networks in which these hosts are embedded contribute to such
751 mechanisms? Addressing such questions with new analytical tools in coexistence research
752 (Saavedra *et al*., 2017; Spaak & De Laender, 2020) could advance our basic understanding of
753 how a variety of direct and indirect interactions affect coexistence among hosts. For example,
754 do symbionts induce indirect interactions among ant hosts? Do ant density-dependent
755 interactions between symbionts (Parmentier *et al.*, 2018) represent a stabilizing higher-order
756 interaction (Grilli *et al.*, 2017)?
757 Insights from this review are restricted and applicable to networks as characterized at the
758 species level, thereby neglecting any intraspecific variation. Following the relevance of
759 ecological and evolutionary determinants, the question remains open as to what degree co-
760 evolutionary dynamics between hosts and their symbiont community occur. As strong
761 selection may act on ant symbionts to bypass host colony defence, cryptic speciation in ant
762 symbionts is expected to be high (Schönrogge *et al.*, 2002; Zagaja & Staniec, 2015; von
763 Beeren, Maruyama & Kronauer, 2015). Symbiont populations may be adapted to an
764 individual host population as was demonstrated in the ant-parasitic syrphid fly *Microdon* and
765 the butterfly *Phengaris* (Elmes *et al.*, 1999; Tartally *et al.*, 2019). Ultimately, population
766 divergence may result in cryptic symbiont species each targeting a different host species.

767 At a higher phylogenetic level, other hymenopteran and insect lineages (Isoptera) provide
768 similar niches to nest symbionts. None of the listed ant symbionts are shared with wasps,
769 solitary and eusocial bees and termites (note that the latter two groups are poorly represented
770 in Europe). Apparently only facultative symbionts (e.g. *Porcellio scaber* in wasp and bee
771 nests for instance) or very generalist entomopathogens such as *Beauveria bassiana* are able to
772 spread across different social insect lineages, but more study is needed to understand the
773 drivers of host–symbiont divergence at these deep phylogenetic levels.
774
775 **VI. CONCLUSIONS**
776 (1) Ant–symbiont networks are particularly interesting to study large-scale patterns and
777 drivers in host–symbiont network topology and symbiont richness as they are extremely
778 diverse and cover the entire mutualism–antagonism continuum. We assembled a complete
779 network of ant–symbiont interactions in Europe and studied the drivers of host specificity,
780 symbiont richness and symbiont sharing in the different interaction sub-networks.
781 (2) We identified 722 ant macrosymbionts which we categorized in five types: (1)
782 myrmecophiles – commensalistic and parasitic arthropods (N = 535); (2) trophobionts –
783 mutualistic aphids, scale insects, plant hoppers and mutualistic Lepidoptera (N = 80); (3)
784 social parasites – parasitic ant species (N = 71); (4) parasitic helminths (N = 22); (5) fungi –
785 parasitic (N = 13) and mutualistic (N = 1).
786 (3) The different types of ant symbionts significantly varied in host specificity. Apart from
787 quantitative differences in host range, we also found clear differences in the average
788 taxonomic/phylogenetic relatedness of the targeted host species for the different types of ant
789 symbionts. The most species rich and best-studied ant genera generally supported the largest
790 number of symbionts, but the different types of symbionts were unevenly distributed across
791 ant genera.

(4) We revealed that the ecological and evolutionary factors which drive symbiont species richness may shift depending on the type of symbiosis. Myrmecophile species richness is mainly determined by ecological drivers, such as colony size, host range and niche width of the host. By contrast, species richness of social parasites is strongly determined by the evolutionary factor host phylogeny.

(5) Ants living in the same biogeographic region shared more symbionts. The sharing of trophobionts, helminths and social parasites, in particular, was also strongly facilitated in phylogenetically related hosts.

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VIII. REFERENCES

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IX. SUPPORTING INFORMATION

Appendix S1. Host–symbiont matrix listing the associations between ants and ant symbionts in Europe. Ant species are listed in columns and symbionts in rows. 1, interaction recorded; 0, no interaction recorded.

Appendix S2. List of literature used to reconstruct the host–symbiont matrix in Appendix S1.

Appendix S3. Host–symbiont matrix for ant hosts with known phylogeny.

Appendix S4. Predictor values of host ant species.

Fig. S1. Correlation between the number of described European species in an ant genus and the number of associated symbionts.

Fig. S2. Number of host species per symbiont type.

Fig. S3. Mean ± SE taxonomic distance of targeted host species for different types of ant symbionts. Symbionts with a single host species were omitted from this analysis. Letter codes refer to Tukey *post-hoc* test. Symbiont types with no letters in common are significantly different ($P < 0.05$).

Fig. S4. Mean ± SE taxonomic distance of targeted host species for different types of ant symbionts. Taxonomic distance of symbionts with a single host species was set at 1.

FIGURE LEGENDS

Fig. 1. Distribution of different types of ant symbionts. Total number of symbionts $N = 722$, number of symbionts per type given in parentheses. Trophobionts are mutualistic, social parasites and helminths are strictly parasitic. Fungi are parasitic, except for the mutualistic species *Cladosporium myrmecophilum*. Myrmecophiles range from commensals to parasites and include parasitoid wasps and flies. Note that three mutualistic Lepidoptera species are classified as trophobionts and six parasitic and commensalistic Lepidoptera species as myrmecophiles.

Fig. 2. Ant–symbiont network displaying the proportional distribution of symbionts across the European ant genera. A multilevel pie chart is given for each ant genus. The size of the outer pie chart corresponds to the total number of associated symbionts (circle size legend in right corner). The size of the inner pie chart is related to the number of symbionts that are not shared with other ant genera (unique symbionts). The proportional distribution of the five types of ant symbionts (see Fig. 1) is given for all associated symbionts (colour segments in outer pie charts) and for the symbionts that are not shared with other genera (colour segments in inner pie charts). The relative proportion of unique symbionts can be deduced by the relative size of the inner circle to the outer circle. The genera are organized in four groups, corresponding to the ant subfamily to which they belong. The genera are connected with lines, of which the width is directly proportional to the number of shared symbionts. The font size of a genus is proportional to its number of described species in Europe.

Fig. 3. Mean ± SE number of host species per symbiont type, controlled for sampling effort. Letter codes refer to Tukey *post-hoc* test. Species with no letters in common are significantly different ($P < 0.05$).

Fig. 4. Mean ± SE phylogenetic distance of targeted host species (based on the phylogenetic tree of Arnan *et al.*, 2017) for different types of ant symbionts. Letter codes refer to *post-hoc* test. Symbiont types with no letters in common are significantly different ($P < 0.05$).

Fig. 5. Ranking of the predictors from the five PGLS models by the corrected Akaike information criterion (AICc). The change in AICc (ΔAICc) when adding or removing a variable from the most optimal model is compared. Predictors included in the most optimal model are removed (ΔAICc positive), whereas those not included are added (ΔAICc negative) to the best model (lowest AICc). The ranking is given for the five PGLS analyses, i.e. with dependent variable the number of symbionts (best model: ~ sample effort + colony size + distribution + habitat), myrmecophiles (best model: ~ sample effort + colony size + distribution + habitat + worker size), trophobionts (best model: ~ sample effort + habitat), social parasites (best model: ~ distribution range) and helminths (best model: ~ sample effort + habitat), respectively. Note that myrmecophiles, trophobionts, social parasites and helminths are four subsets of all ant-associated symbionts.

Fig. 6. Relative importance of the significant predictor matrices explaining the dissimilarity in symbiont communities across different ant species. Rankings are given for predictors explaining overall dissimilarity (1–similarity) in symbiont composition, and for dissimilarity in subsets of symbiont composition: myrmecophiles, trophobionts, social parasites, helminths and parasitic fungi, respectively. Note that myrmecophiles, trophobionts, social parasites, helminths and parasitic fungi are subsets of all ant-associated symbionts. The allocated contribution (sequential R^2) of the different distance matrices (indicated with Δ) or the matrix capturing the combined sample effort of a pair of host species to the explained variation of the

MRM models is estimated with the lmg metric. The error bars are 95% confidence intervals produced using 1000 bootstrap replicates. The combined sample effort of a pair of host species was negatively correlated with their dissimilarity in symbiont composition. The dissimilarity matrices of all other predictors were positively correlated with dissimilarity in symbiont composition. Significance levels of the predictors were tested with a permutation test (N = 9999; ***, $P < 0.001$; **, $P < 0.01$; *, $P < 0.05$; ˙, $P < 0.10$).

FIGURES

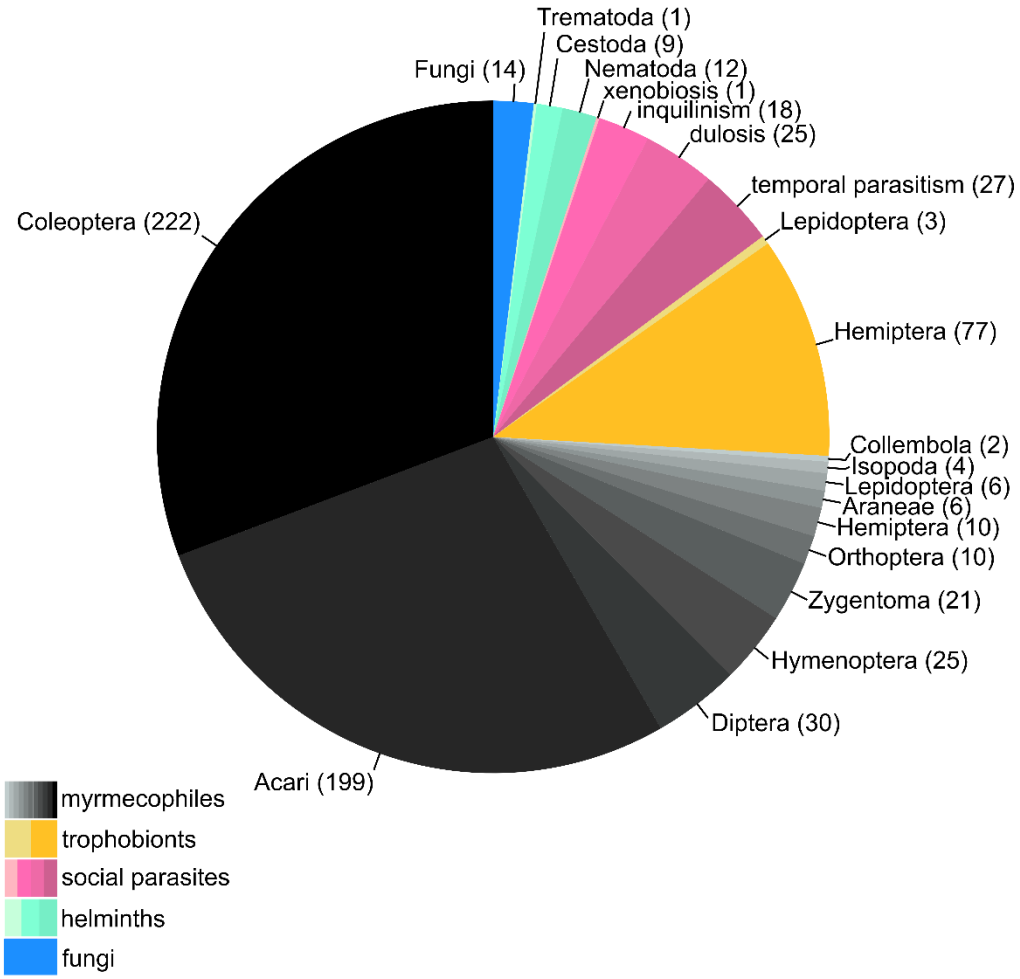
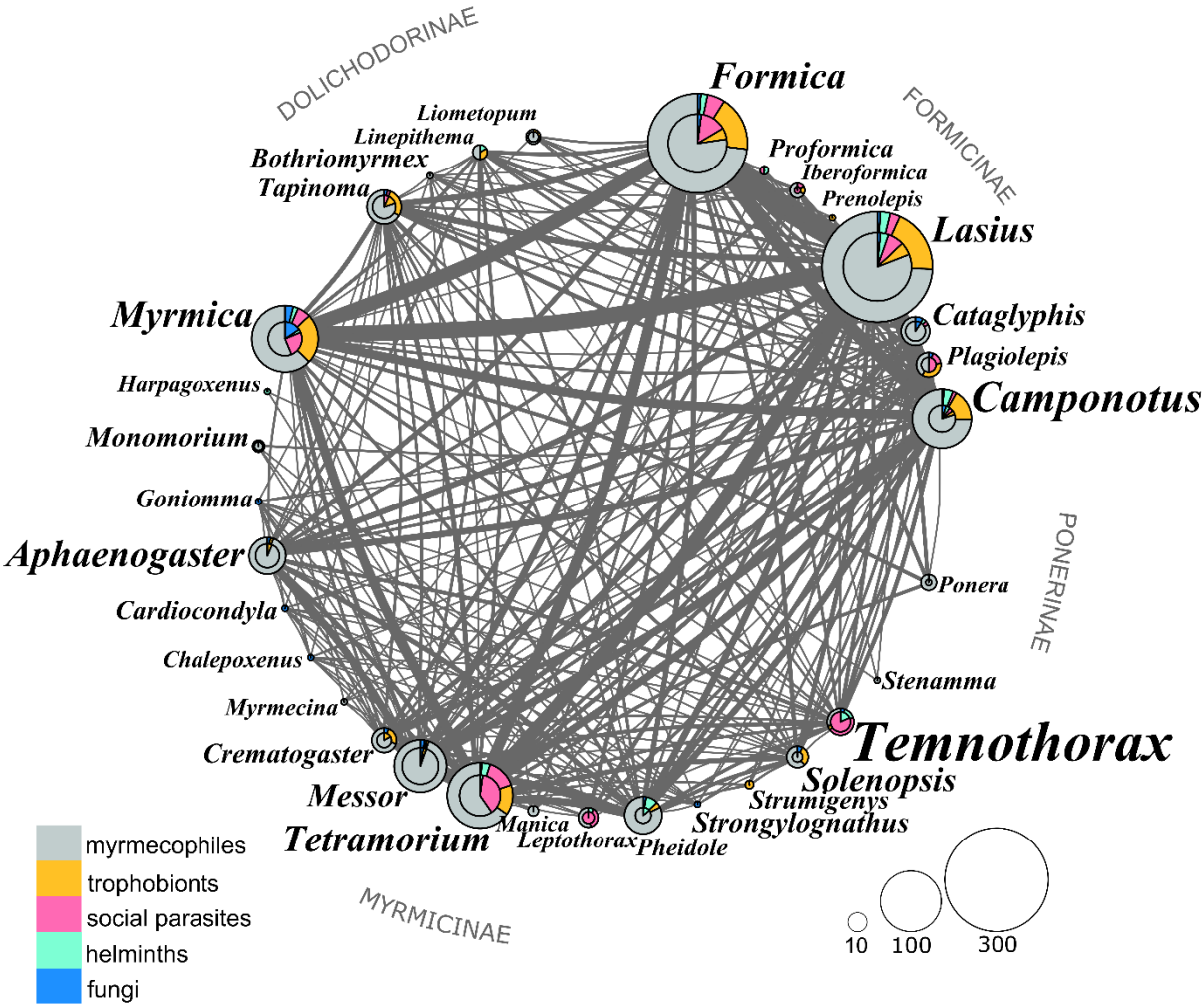
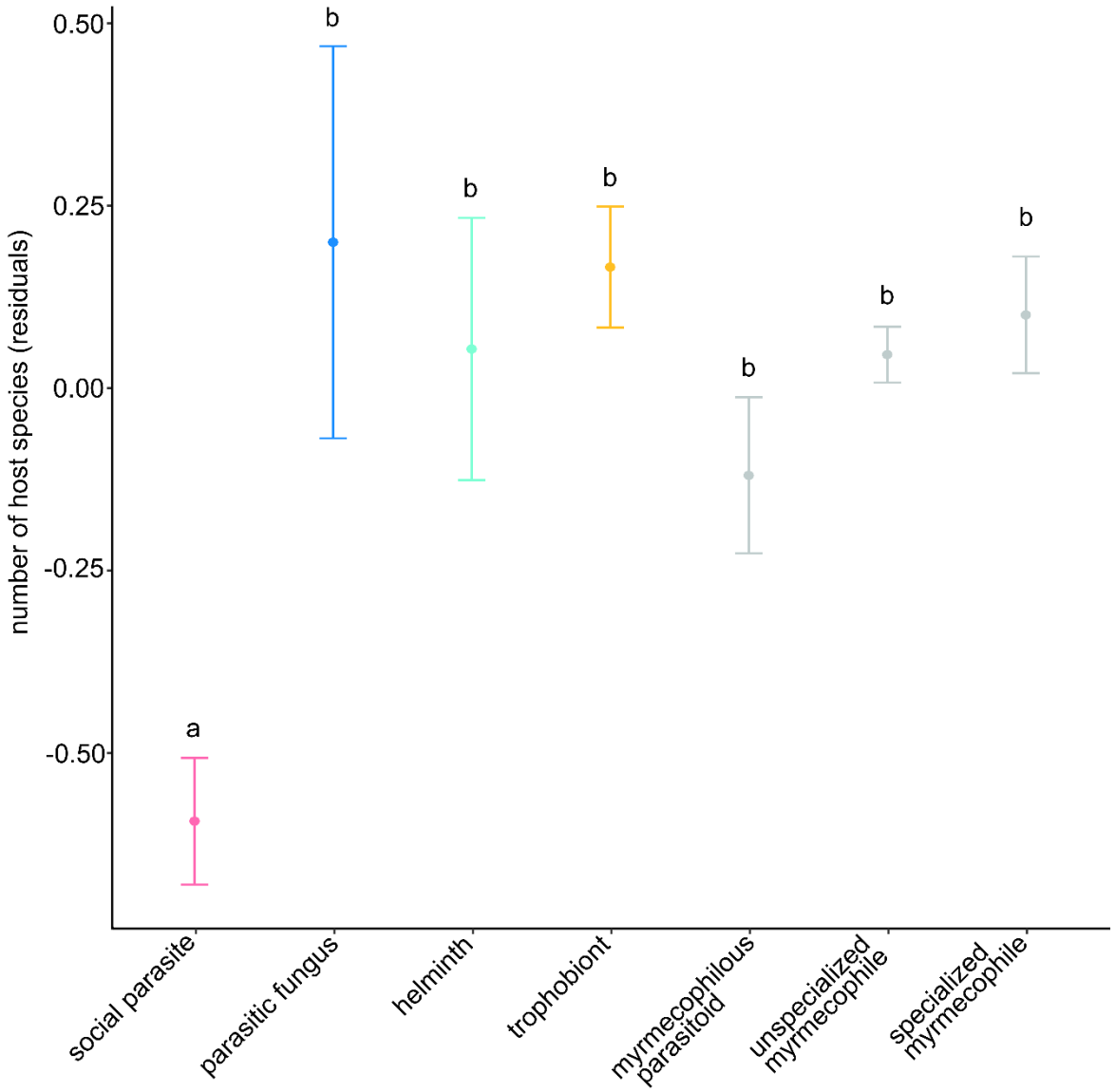


Fig. 1



1852

1853 Fig.2



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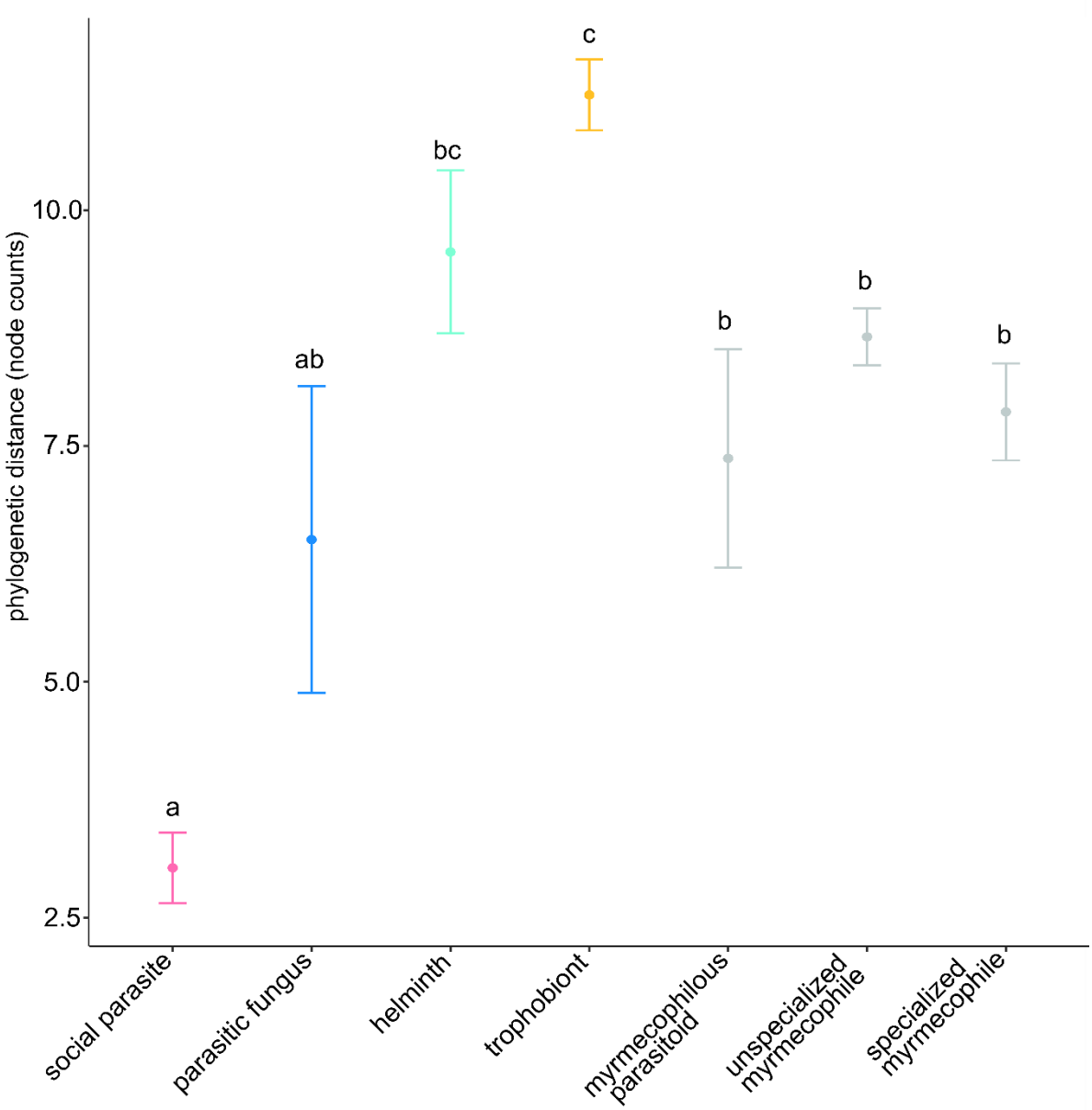

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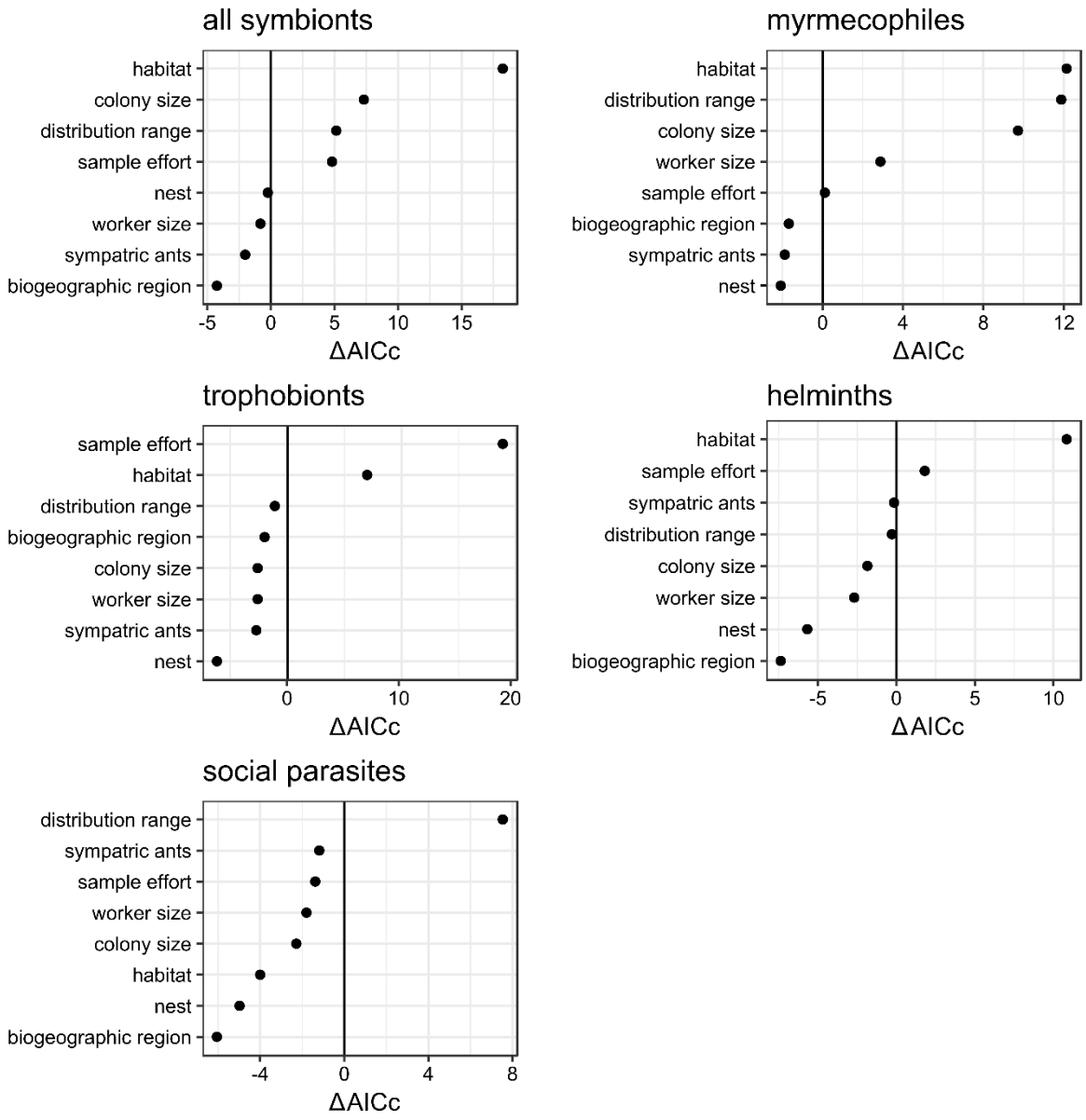

1860

1861 Fig. 5

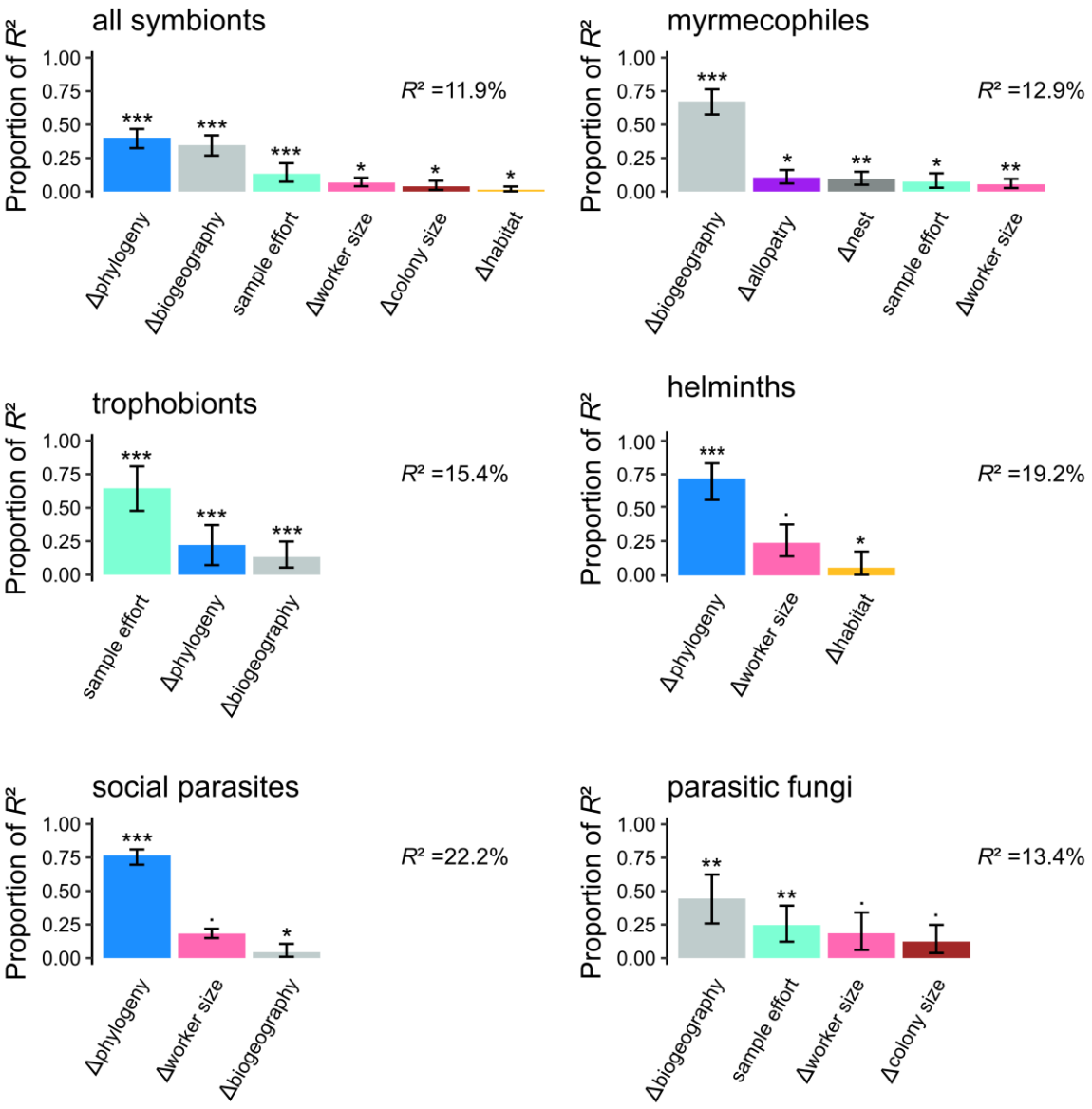
all symbionts
Proportion of R²
1.00
0.75
0.50
0.25
0.00
R² =11.9%
***
***
***
*
*
*
Δphylogeny
Δbiogeography
sample effort
Δworker size
Δcolony size
Δhabitat
myrmecophiles
Proportion of R²
R² =12.9%
***
*
**
*
**
Δbiogeography
Δallopatry
Δnest
sample effort
Δworker size
trophobionts
Proportion of R²
R² =15.4%
***
***
***
sample effort
Δphylogeny
Δbiogeography
helminths
Proportion of R²
R² =19.2%
***
.
*
Δphylogeny
Δworker size
Δhabitat
social parasites
Proportion of R²
R² =22.2%
***
.
*
Δphylogeny
Δworker size
Δbiogeography
parasitic fungi
Proportion of R²
R² =13.4%
**
**
.
.
Δbiogeography
sample effort
Δworker size
Δcolony size

Fig. 6

TABLES

1868 Table 1. Overview of the different types of ant symbionts found in Europe.

Symbiont type	General description	Representatives and strategies	Ref.
MYRMECOPHILE	A diverse group of arthropods that mostly live inside ant nests. The life strategies of these organisms range from commensalism to specialized parasitism; there are no mutualists in this group. Representatives in many arthropod orders, but beetles and mites are the most diverse. Also known as ant guests.	- **unspecialized myrmecophiles**: poorly integrated in the colony and may provoke aggression. Very similar in behaviour and morphology to free-living relatives. Do not rely on advanced chemical deception. - **specialized myrmecophiles**: accepted in the colony by being groomed, fed or transported. Typically possess advanced glandular structures (trichomes) or specialized behaviour to deceive the host. - **myrmecophilous parasitoids**: wasps and flies of which the larvae parasitize ant workers, ant larvae or possibly other myrmecophiles. Eventually kill the host. Adult parasitoids do not live in the nest.	1–6
TROPHOBIONT	Mutualistic arthropods that provide sugary honeydew in exchange for protection and hygienic services. Mostly live outside the nest.	- **Hemiptera**: aphids, scale insects and planthoppers. - **Lepidoptera**: mutualistic caterpillars permanently living outside the nest.	1
SOCIAL PARASITE	A group of ants that parasitize other ant species.	- **xenobiosis:** parasitic ants that construct a nest inside other ant nests, but raise their own brood. - **temporary parasitism**: a parasitic queen usurps a host colony and exploits the host work force to establish her own colony. Parasite workers gradually substitute the host worker force. - **dulosis (slavery)**: a parasite colony is established as in temporary parasitism, but here the workers of the parasitic species will raid pupae of other ant species. Workers which will emerge from these pupae will do most of the tasks in the colony. - **inquilinism**: parasitic queens permanently exploit a host colony. The parasitic queen produces only sexuals, not workers.	7
HELMINTH	Endoparasitic worms	- **nematodes (Nematoda)**: the juveniles (dauers) of some groups, such as the Rhabditidae and Diplogastridae, live in the postpharyngeal glands of their ant host and are considered weak parasites. Mermithid nematodes develop in the haemocoel of the ant, may cause morphological changes in the host, and ultimately kill the host upon emergence. Other hosts, such as oligochaetes, may be necessary to complete the life cycle of mermithids.	8–9

		- **<u>flukes (Platyhelminthes: Trematoda)</u>**: *Dicrocoelium* is a trematode whose definitive hosts are grassland vertebrates. The eggs are released along with the faeces and eaten by snails. Ants serve as the second intermediate host of the parasite and become infected by ingesting snail slime. The parasite induces behavioural changes in the ant which then climb to the top of grass stems where they are ingested by the definitive host. - **<u>tapeworms (Platyhelminthes: Cestoda)</u>**: cestodes are infamous parasites that live in the digestive tract of vertebrates. These tapeworms have a life cycle with multiple hosts and ants may serve as an intermediate host.	
FUNGUS	A diverse group of mainly ant-specific ecto- and endoparasites.	- **<u>parasitic fungi</u>:** Laboulbeniales are ectoparasites that do not kill their host. They produce a multicellular thallus externally attached to the integument of the host ant. *Myrmicinosporidium durum* is an endoparasitic fungus which ultimately kills its host. *Pandora formicae* is a well-known entomopathogenic fungus, that manipulates its ant host to climb the vegetation. The ant attaches itself to the distal part of leaves with its mandibles and dies of the infection. - **<u>mutualistic fungi</u>:** *Cladosporium myrmecophilum* provides stability and structure to the carton nests of *Lasius fuliginosus*.	10, 11

1869 1, Hölldobler & Wilson (1990); 2, Kronauer & Pierce (2011); 3, Elizalde *et al*. (2018); 4, Pérez-Lachaud *et al*. (2019); 5, Parmentier (2020); 6, Kistner (1982); 7, Buschinger
1870 (2009); 8, Poinar (2012); 9, Demartin (2018); 10, Espadaler & Santamaria (2012); 11, Maschwitz & Hölldobler (1970).

Table 2. Estimates for the predictors of the top-ranked PGLS analyses (ΔAICc < 2). The subset of best models is given for the analyses with total number of (1) symbionts, (2) myrmecophiles, (3) trophobionts (4) social parasites and (5) helminths as dependent variable. Significant estimates indicated in bold (***, *P* < 0.001; **, *P* < 0.01: *, *P* < 0.05; ˙, P < 0.10).

	intercept	colony size	sample effort	biogeography	distribution	habitat	sympatric ants	nest type	worker size	d.f.	AICc	weight	lambda
all symbionts													
	6.48	**0.82*** **	**0.89** **		**0.70** ***	**+*** **				7	375.3	0.33	0.54
	7.93	**0.71*** **	**0.84** **		**0.74*** **	**+*** **		+˙		10	375.5	0.30	0.52
	6.85	**0.82*** **	**0.82** **		**0.77*** **	**+*** **			0.31	8	376.0	0.22	0.44
	8.20	**0.70*** **	**0.77** **		**0.80*** **	**+*** **		+˙	0.26	11	376.8	0.15	0.41
myrmecophiles													
	6.29	**0.81*** **	0.43		**0.95*** **	**+*** **			**0.45** *	8	299.0	0.31	0.00
	6.64	**0.94*** **			**1.17*** **	**+*** **			**0.46** *	7	299.1	0.29	0.00
	7.95	**0.75*** **			**1.20*** **	**+*** **		+˙	**0.44** *	10	300.4	0.15	0.00
	7.56	**0.57*** **	**0.66** *	**+*** **	**0.80*** **	**+*** **			**0.57** *	12	300.7	0.13	0.32
	6.21	**0.81*** **	0.45		**1.10*** **	**+*** **	-0.22		**0.42** *	9	300.9	0.12	0.00
trophobionts													
	2.93		**0.77*** **			**+*** **				5	131.2	0.42	0.73
	3.14		**0.64*** **		**0.20*** **	**+*** **				6	132.3	0.24	0.60
	3.52	**0.22** **	**0.42** *		**0.31*** **	**+*** **				7	133.0	0.18	0.36
	3.06	**0.11** **	**0.26** ***			**+*** **				6	133.2	0.16	0.68
social parasites													
	1.34				**0.27** **					2	75.5	0.23	1.00
	1.19		**0.26** **							2	75.9	0.19	1.00
	1.25						**0.22** **			2	76.4	0.15	0.83
	1.30				**0.17** **		0.11			3	76.7	0.12	0.94
	1.27		0.13		**0.16** **					3	76.9	0.11	1.00
	1.21		**0.16** **				0.11			3	76.9	0.11	0.93
	1.29				**0.26** **				-0.10	3	77.3	0.09	0.98
helminths													
	1.81		**0.14** *			**+*** **				5	31.7	0.18	0.91
	1.83		**0.11** *			**+*** **	0.10			6	31.8	0.16	0.88
	2.01					**+*** **	0.13˙			5	31.9	0.16	0.85
	1.87		0.11		**0.11** **	**+*** **				6	32.0	0.15	0.88
	2.07				**0.14** **	**+*** **				5	32.1	0.14	0.87

	2.07			+***		4	33.5	0.07	0.88
	1.82	-0.06	**0.16***	+***		6	33.5	0.07	0.94
	1.83	-0.07	**0.14***	+***	0.10	7	33.5	0.07	0.94

1875